THINHEADS, THICKHEADS AND AIRHEADS - FUNCTIONAL CRANIOLOGY OF SOME DIPROTODONTIAN MARSUPIALS.

PETER F. MURRAY

Northern Territory Museum,
P.O. Box 2109, Alice Springs, NT 0875, Australia.

ABSTRACT

The development of complex air cells surrounding the internal brain capsule in diprotodontid, palorchestid and thylacoleonid marsupials is related to a pronounced allometric differential between brain volume to body size resulting in independent growth programs for the inner and outer table of the neurocranium. The dimension of the inner table is directly determined by brain volume and the outer table dimension is determined by jaw adductor mass which increases in relation to overall body size. In large diprotodontids, the presumptive ectocranial area provided by expansion of the neural capsule due to brain growth would provide insufficient external surface for the attachment of the adductor muscles. Diprotodontid marsupials circumvent this potential limitation to the attainment of large body size by independent expansion of the outer table of the neurocranium in proportion to the surface area required by the musculature. The majority of large placental herbivores have responded to the same constraint by a reorganization of the adductor muscle configuration.

KEYWORDS: endocranial sinuses, Thylacoleonidae, Diprotodontidae, Vombatidae, Palorchestidae, allometry, functional craniology, jaw musculature.

INTRODUCTION

Owen (1877) was first to draw attention to the presence of large endocranial air sinuses surrounding the lateral and posterior portions of the neural capsule in certain marsupials. Van der Klaauw (1931) described the relationship of some of these sinuses within the squamosal, occipital and alisphenoid in relation to the anatomy of structures surrounding the middle ear of marsupials and other mammals. Klaauw's (1931, 1946, 1948-52) observations form the anatomical basis of numerous subsequent studies of mammalian cranial form.

It seems, however, that the truly remarkable extent to which certain large marsupial crania are composed of little more than air cells has eluded anatomical investigation. Rather similar developments had been noted in the frontoparietal region of elephants (Osborne 1942) and in suids. Gregory (1903) related the development of the frontal dome in the elephant to the separation of the inner and outer table of the braincase in order to support the trunk musculature

anteriorly and the nuchal musculature posteriorly (see Gregory 1974: Figs 21-32, 21-33).

As well as being relatively more extensive than in elephants and pigs, the neurocranial sinuses of *Palorchestes* Owen, *Kolopsis* Woodburne, *Neohelos* Stirton, *Zygomaturus* Mcleay, *Diprotodon* Owen and *Thylacoleo* Owen originate from different regions of the cranium. Thus, while it is likely that a general explanation of the sinuses applies to both marsupials and placentals, the reasons for the developments differ for each group. The more specific details of sinus development in the diprotodontians are sought in this investigation.

The particular manifestation of these endocranial sinuses in the Thylacoleonidae, Diprotodontidae and Palorchestidae are considered to have systematic importance (Klaauw 1931, Ride 1964, Aplin 1987). Their presence moreover, constitutes an anatomical curiosity deserving, at least, a description sufficiently detailed and accurate to attract the attention of other craniometrists and functional anatomists better equipped to make broader and more pertinent

observations than the preliminary study presented here.

In this investigation I describe the endocranial sinuses in a representative sample of diprotodontian genera. Several variables that appear to be related to the development of the condition are considered and a hypothesis explaining the manifestation in terms of these variables is presented.

METHODS AND MATERIALS

The investigation uses proportional comparisons of cranial components in a series of living and extinct diprotodontians. A hypothetical growth series of the extinct genus *Kolopsis* was reconstructed from late Miocene Alcoota Local Fauna (LF) material for comparison with a placental series of *Bos taurus* Linnaeus, the domestic cow.

The observations to follow are based on fossil crania with natural breaks exposing the sinuses to view, thus allowing an occasional accurate measurement. While such information is adequate for the formulation of a hypothesis, the data may not be deemed suitable for verification. I envision that such a study might require sophisticated techniques such as radiographic serial reconstruction, tomography or sonographic probing combined with computerized data points for accurate computations. Although such an investigation is beyond the means of my current situation, the observations from this cruder data set indicate that more technical applications are feasible and that the results might prove interesting.

Crania of the following living marsupial genera were employed in the investigation: *Didelphis* Linnaeus, *Marmosa* Gray, *Cercartetus* Burmeister, *Pseudocheirus* Ogilby, *Trichosurus* Lesson, *Phascolarctos* Blainville, *Phalanger* Storr, *Lasiorhinus* Gray, *Vombatus* Geoffroy and *Macropus* Shaw. The fossil material includes: Palorchestidae: *Propalorchestes* Murray (NTM P895-1, P8552-10); Diprotodontidae: *Neohelos* (NTM P8695-38, P8551-13, CPC F23038), *Kolopsis* (NTM P1007, P8893, P92185, P92186, P92187), *Zygomaturus* (unregistered specimen, Victoria Fossil Cave) and *Thylacoleo* (SAM P16730). Abbreviations: NTM, Northern Territory Museum; CPC, Commonwealth Palaeontological Collection; SAM, South Australian Museum. Marsupial systematics follows Aplin and Archer (1987).

ANATOMICAL DESCRIPTION

Endocranial sinuses enveloping all but the ventral surface of the internal capsule of the brain appear to be found among only the larger palorchestid, diprotodontid and thylacoleonid marsupials of the Infraorder Vombatomorphia. Other diprotodontians show various degrees of sinus development, particularly within the squamosal and sometimes within the frontals, but not within the posterodorsal components of the neurocranium, e.g. the parietals, interparietal and supraoccipital. The primary sinus development of the squamosal region is termed the Epitympanic Sinus (Klaauw 1931). An anterior epitympanic sinus is present in nearly all Australidelphian marsupials (Ride 1964). A posterior component of the epitympanic sinus is largely confined to the diprotodontians, among which, in living forms, its greatest degree of development is found in vombatids (Figs 1, 2).

Even in *Lasiorhinus*, in which the anterior and posterior epitympanic sinuses are greatly enlarged, only the squamosal portion of the internal capsule is separated from its outer table (Fig. 2). In the extinct palorchestids and diprotodontids the sinuses continue around the dorsal surface of the brain capsule resulting in its virtual suspension by thin bony septa within a series of large airspaces.

These aircells are interconnected by small openings and contain emissary venous channels that anastomose with venous intracranial sinuses (greater petrosal and sigmoid). Diploic emissaries associated with the postglenoid canals may have passed through the epitympanic fenestra, a large opening in the superficies meatus that leads directly into the epitympanic sinuses.

It can be seen that there are three basic states of sinus development in diprotodontians: these are characterized in the title as "thinheads, thickheads and airheads". In the species with thin cranial bones, for example phalangerids, macropodids and *Phascolarctos*, sinus development is confined to a small group of coalesced diploe in the squamosal lamina (Fig. 3). In thickheaded forms (*Lasiorhinus*, *Vombatus*), large epitympanic sinuses are present but are entirely confined to the squamosal. However, the parietal bones are greatly thickend, with the inner and outer tables being widely separated by intervening diploe. In the airheads (zygomaturines, palorchestines) the region corresponding to the parietal diploe in vombatids is entirely pneumaticized into larger cells with the septa

corresponding to the sutural contacts of the parietal and squamosal (Fig. 2).

In terms of body weight, the diprotodontian species with thin cranial walls are small to medium-sized animals with relatively large brain volumes (Moeller 1973). *Lasiorhinus* and *Vombatus*, which possess thick-walled crania, are among the heaviest living marsupials and also have relatively large brain weights. The forms with greatly enlarged intracranial air cells are all extinct and cannot be directly compared by weight with the others. However, all of them were from about twice to over 10 times more massive than any living marsupial.

About a half or slightly more of the total coronally sectioned width of a thin-walled cra-
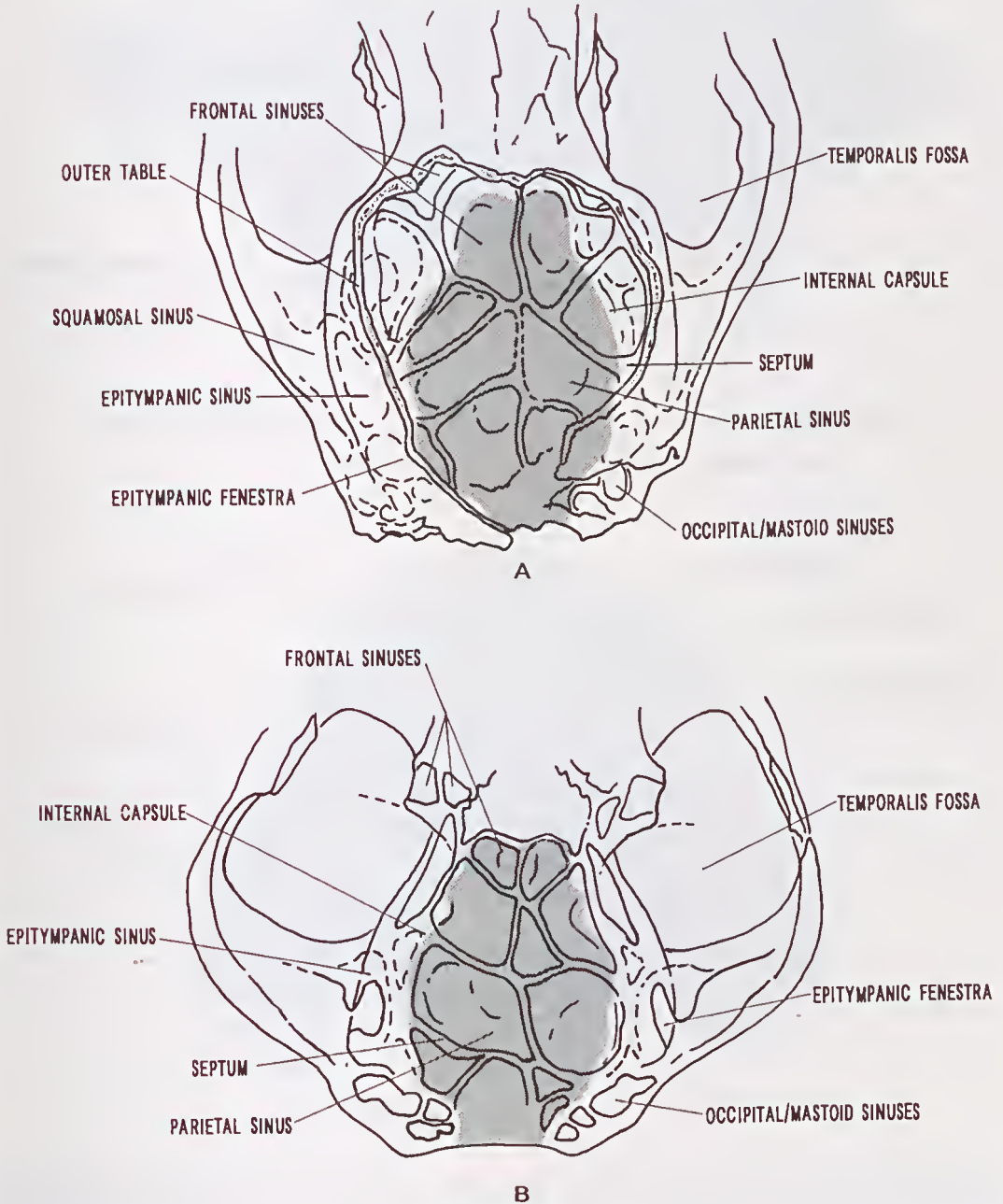

Fig.1. Line drawing of dorsal aspect of pneumatieized diprotodontian crania showing form and extent of air cells surrounding the neural eapsule; A, Miocenc diprotodontid *Kolopsis torus* 0.5X; B, Late Pleistocene thylacoleonid *Thylacoleo carnifex* 0.5X.

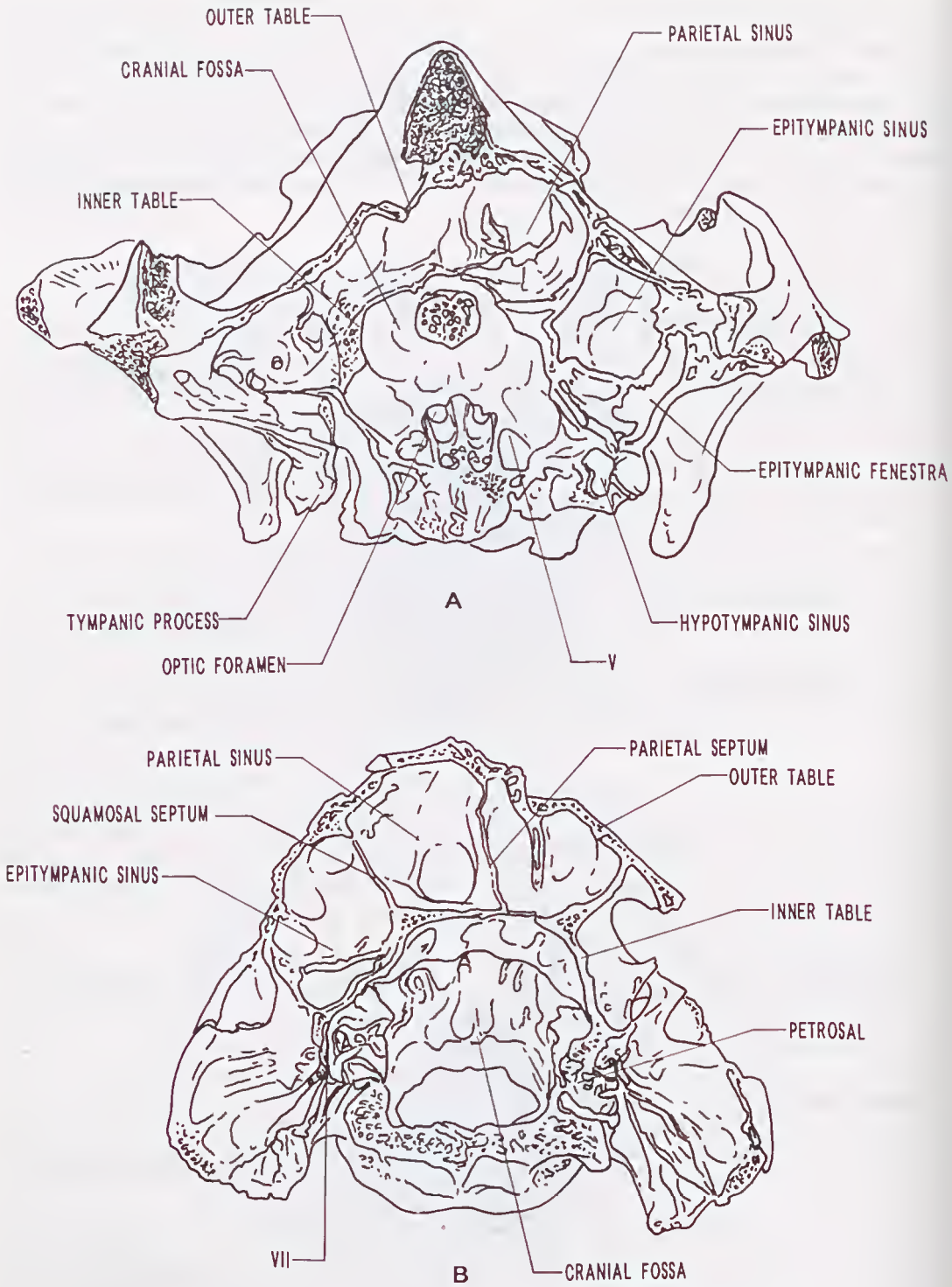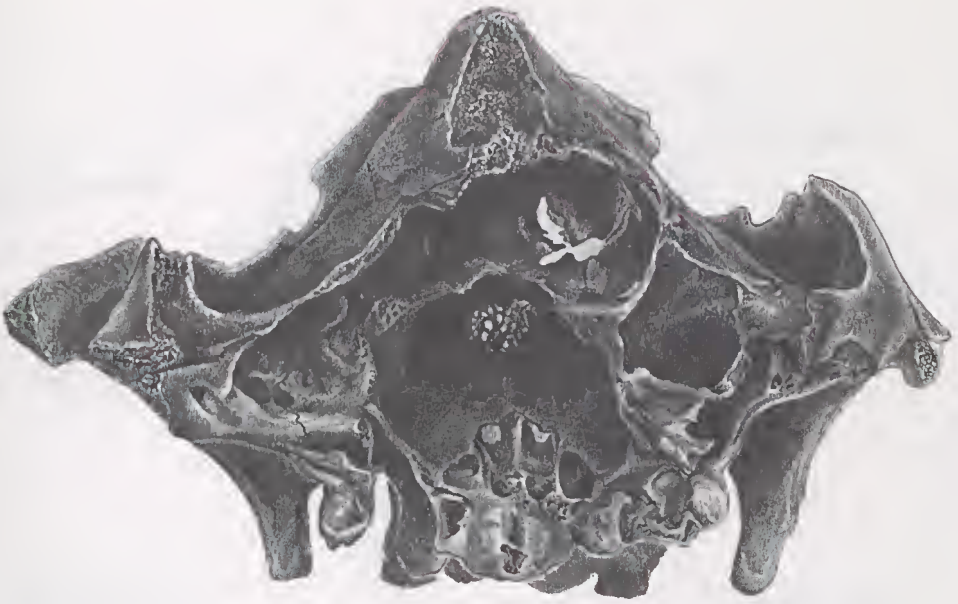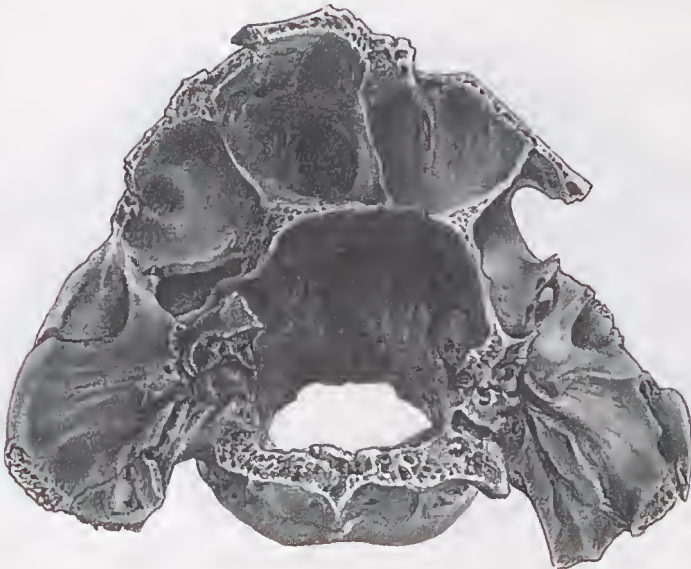**Fig.2. A-B,** drawings of **A,** naturally broken coronal section through the highly pneumaticized cranium of Miocene palorchestid *Propalorchestes novaculacephalus* Murray, looking into anterior portion 0.5X; **B,** *P. novaculacephalus,* looking into the posterior portion 0.5X.

a

b

Fig. 2. A-B, (cont.): In A-B the large air cells dorsal and lateral to the internal capsule of *Propalorchestes* correspond to the thickened diploeic region dorsally (the former being fusions of the many cells of the latter) and large epitympanic sinuses laterally in *Lasiorhinus* (C-D).
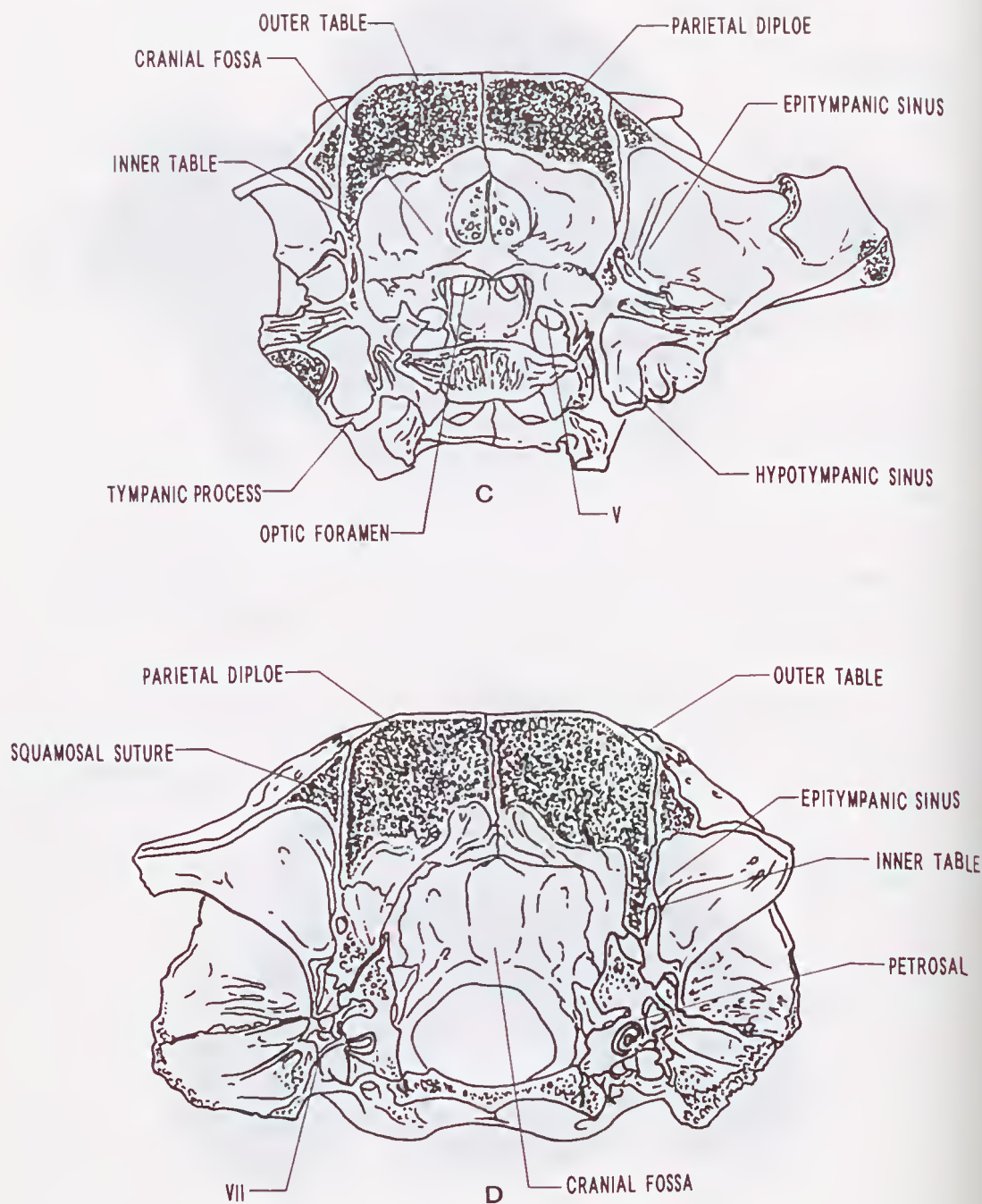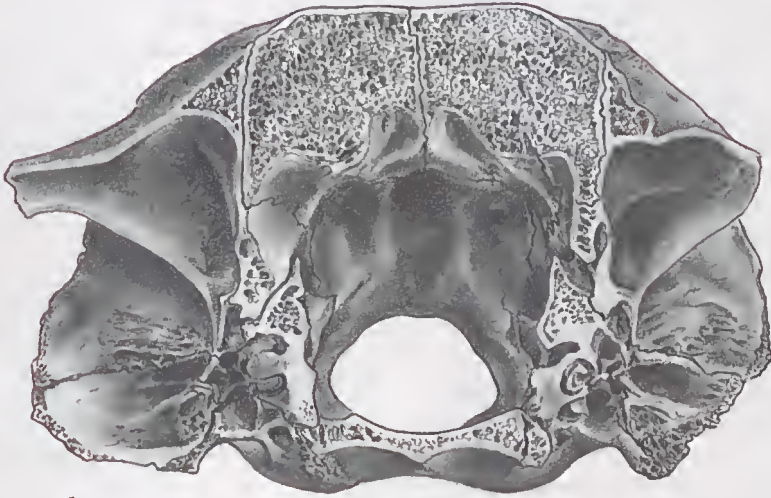
Fig.2. C-D, drawings of C, coronally sectioned cranium of living vombatid *Lasiorhinus latifrons* (Owen), looking into the anterior portion 1.0X; D, *Lasiorhinus latifrons*, looking into the posterior portion 1.0X.

c

d

Fig. 2. C-D (cont.): In A-B the large air cells dorsal and lateral to the internal capsule of *Propalorchestes* correspond to the thickened diploeic region dorsally (the former being fusions of the many cells of the latter) and large epitympanic sinuses laterally in *Lasiorhinus* (C-D).

nium is represented by the endocranial space occupied in life by the brain and its associated tissues. In the thick-walled crania, about a third of the total width of the cranium is endocranial space, and in the pneumaticized cranium less than a fourth of its total width is represented by endocranial space (Figs 4, 5). Plots of the width of the endocranial space to the width of the temporalis fossa yields a coefficient of about 0.45, whereas the trend of outer braincase dimensions to width of the temporalis fossa is much steeper, with a coefficient of about 0.80 (Fig. 6).

A divergence in the trends, indicating a transition to allometric growth of the outer table in relation to the internal capsule, becomes apparent at the point at which the internal cranial dimension of the large extinct diprotodontians approximates the external braincase dimension of the largest living representatives. This transition, which is simply a manifestation of the surface to volume functions of the inner and outer tables, is not at all apparent from the external aspect of the crania, which retain very similar adductor mass to braincase proportions among species ranging from mouse-sized *Cercartetus* to rhino-sized *Zygomaturus*.

The linear proportional relationships observed in a phyletic series of diprotodontian marsupials is similarly reflected in the ontogeny of the diprotodontid species *Kolopsis torus* (Fig. 7) which is considered typical of the family. In the cranium of the placental herbivore *Bos taurus*, there is a marked change in the proportions of the splanchnocranium relative to the neurocranium during the later stages of maturation. The conspicuous proportional sliding between the neural and facial components of the cranium is characteristic of the majority of large placental herbivores (Klaauw 1942).

The anatomical observations suggest the following: 1) the endocranial sinuses are associated with large-bodied diprotodontian marsupial species, in which the external surface of the braincase remains co-linear in relation to increased body size (the ectocranial surface remains proportional to the square of any of its linear dimensions), whereas the internal capsule of the braincase increases proportionally to the cube of any of its linear dimensions; 2) a tendency toward expansion of the outer table away from the inner table of the brain case is incipiently present in the larger, thin-skulled forms (e.g. *Phascolarctos*) and definitely manifested in the thick-skulled vombatid species; and 3) externally, the

diprotodontians retain a linear proportional relationship between the neural and facial components of the cranium, both phyletically and ontogenetically, in contrast to placental herbivores of equivalent size. Internally, the volume of the neural capsule of large vombatomorphs is somewhat smaller than in an equivalent-sized placental herbivore.

SINUS DEVELOPMENT

Two lines of evidence show the process of sinus development in the large marsupial herbivores. The evolutionary process is suggested by the presence of a thickened diploic layer in the larger living diprotodontian species. *Phascolarctos, Lasiorhinus* and *Vombatus*, an exception being the large living *Macropus* species. The ontogenetic development is shown in a series of immature *Kolopsis torus* Woodburne specimens.

The formation of intracranial sinuses is thoroughly documented (Moss and Young 1960). Their development relates primarily to the progressive separation of the inner and outer tables of the braincase. As these separate, the bone thickens through the formation of a diploic layer. The small airspaces within the diploic layer then coalesce into increasingly larger spaces until the region is fully pneumaticized.

In *Lasiorhinus*, the cranial vault has attained a pre-pneumatic stage of inner and outer table separation similar to that of an immature *Kolopsis torus*. In *Kolopsis*, the process of pneumatization of the parietals becomes apparent when the M^5 has begun to emerge from its crypt. As the animal matures, the inner and outer table become increasingly separated; the inner capsule remains in intimate contact with the brain and the outer table continues to expand in proportion to the enlargement of the splanchnocranium and zygomatic arches.

FUNCTIONAL CRANIOLOGY

Moss and Young (1960) outlined the principles of differential growth of the mammalian cranium, emphasizing the influences of soft tissue growth and function on various cranial components. Primary among these are the outer table, diploe and inner table components of the neurocranial plate that grow independently of one another, functionally dissociating in response to their respective soft tissue demands. The inner
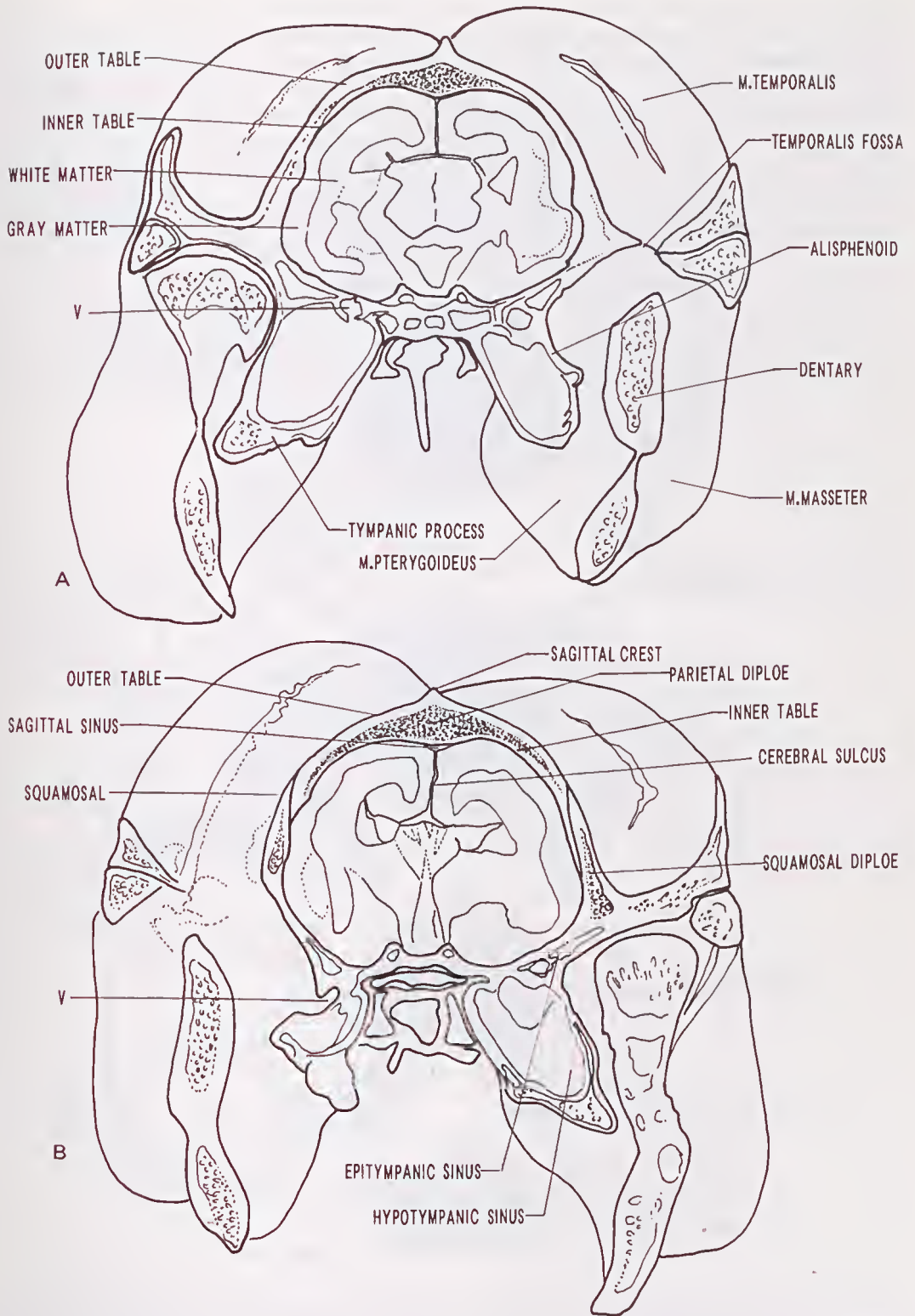
Fig. 3. Coronal section through the comparatively thin-vaulted neurocranium of the Koala, *Phascolarctos cinereus* (Goldfuss), showing soft tissue relations of the braincase; A, looking anteriorly; B, looking posteriorly; note the development of a thin diploic layer, presence of small squamosal epitympanic sinuses and the approximately equal-sized masses of the m. temporalis amd m. masseter.

table grows in reponse to brain growth and is highly sensitive to changes in brain size and shape throughout the lifetime of the animal. The outer table responds to the inereasing demands of scalp tissues in general and speeifically to the requirements of the jaw adductor museles. The diploe intervene in proportion to the extent of functional dissoeiation between the inner and outer table. If the dissociation is extensive, large sinuses develop within the diploie layer as a result.

Consequently, the presenee of large neuroeranial sinuses in gigantie marsupial her-bivores are readily explained by differential growth between the inner table whieh forms the neural capsule and is under the direet influenee of brain growth, and the outer table whieh is under the direet influenee of ectocranial tissue demands. In the earliest stage of maturation in the fossil sample (*Kolopsis torus*), the inner and outer braineare are separated by a thin diploie
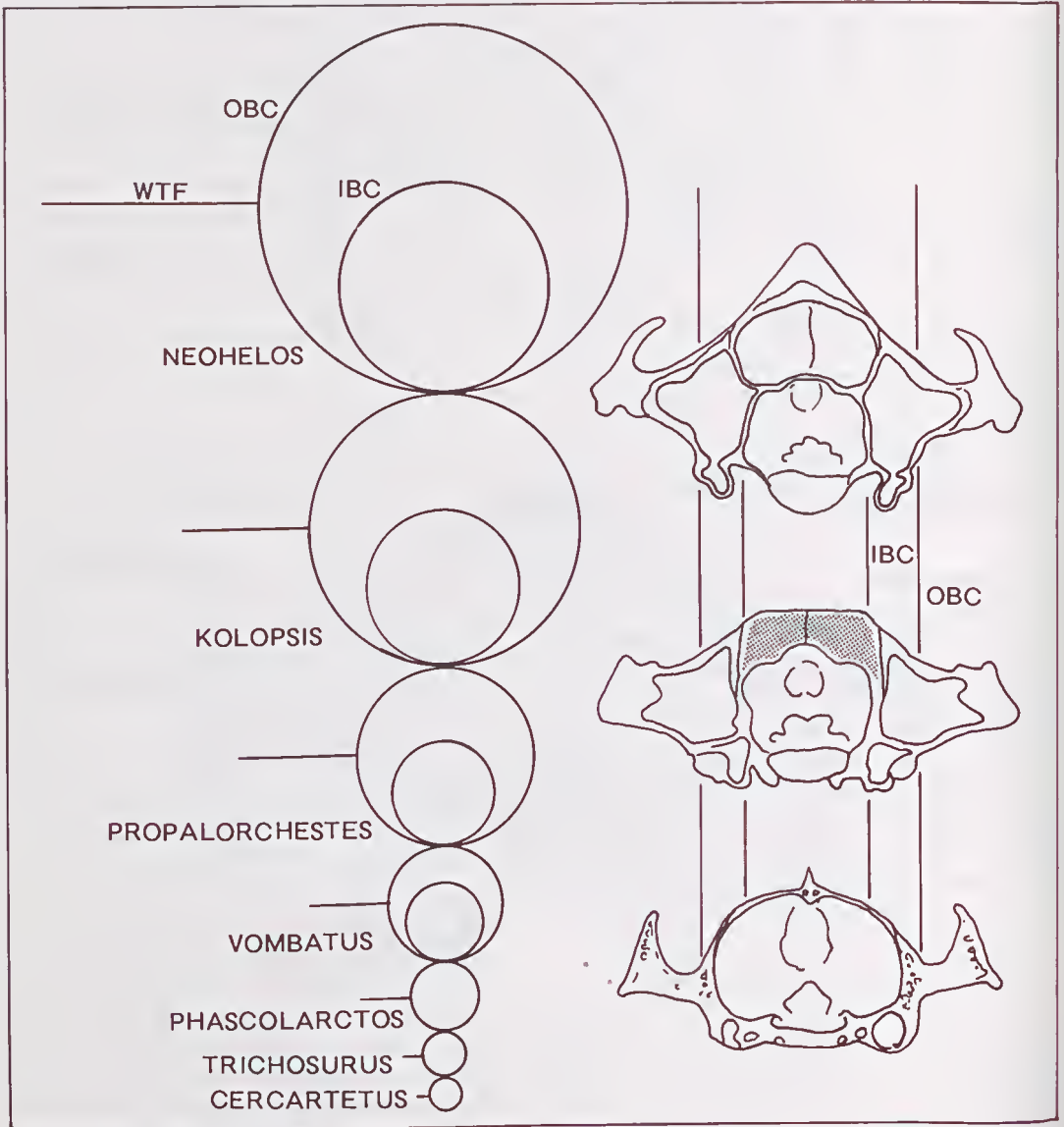
Fig. 4. Illustration of the relative extent of separation of the outer table (**OBC**) from the inner brain eapsule (**IBC**) in a series of diprotodontian marsupials; line labelled **WTF** represents the width of the temporalis fossa in each genus. Note the differential in brain size (inner circle) relative to outer braincase size increases dramatically with the size of the animal, indicating a marked allometry in growth. Figures to the right are scaled to equivalent bizygomatic width: below, brushtailed possum, *Trichosurus*; middle, hairy-nosed wombat, *Lasiorhinus*; above, marsupial tapir, *Propalorchestes*. Abbreviations:**OBC**: outer table: **IBC**, inner brain eapsule; **WTF**, width of temporalis fossa.
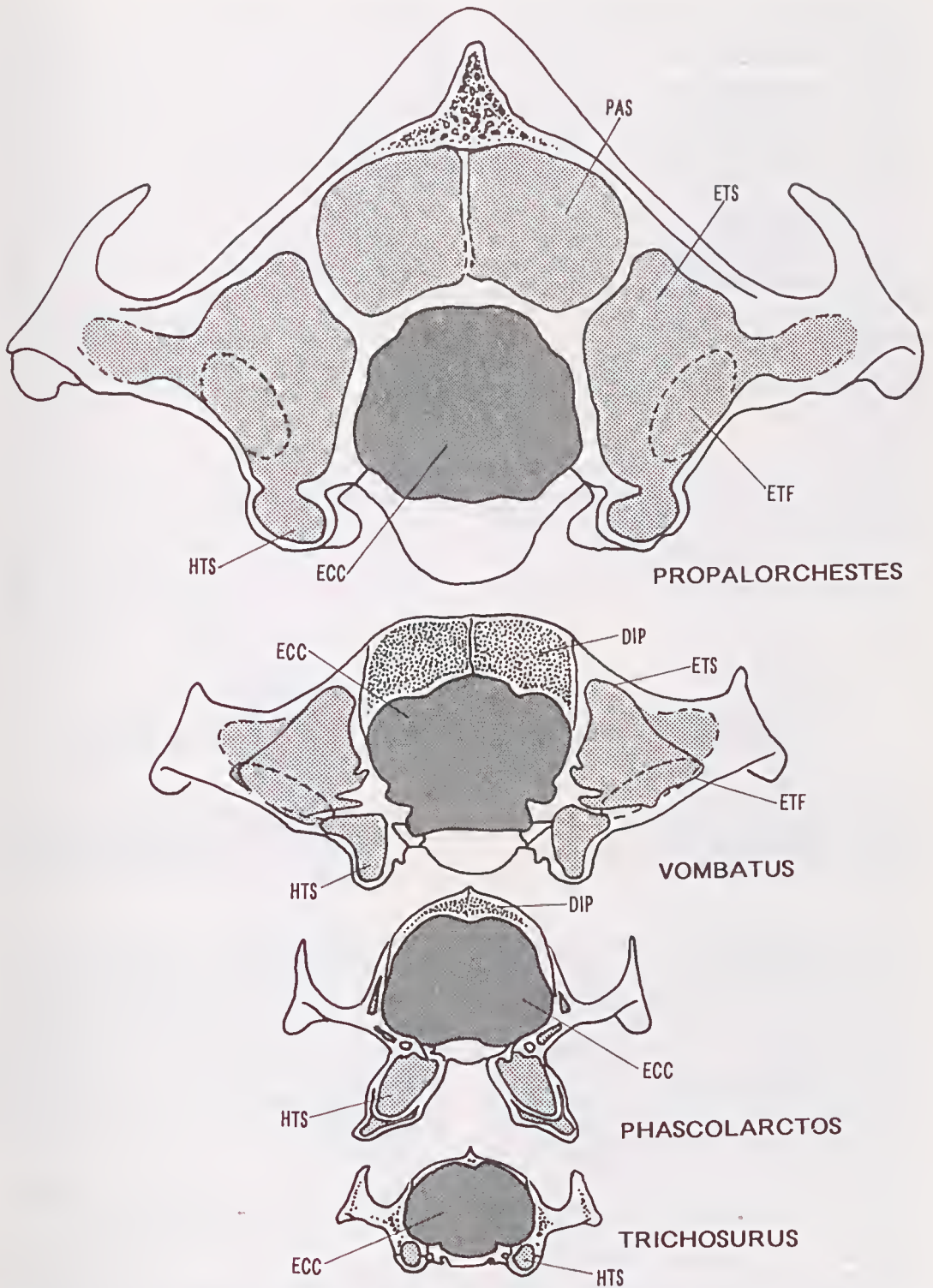
Fig. 5. Scale representation of size of neural capsule to size of the external braincase in a representative series of diprotodontian marsupials; note thin diploic layer in *Trichosurus*; Abbreviations: **ECC**, endocranial cavity; **DIP**, diploe **ETF**, epitympanic fenestra; **ETS**, eptympanic sinus; **HTS**, hypotympanic sinus; **PAS**, parietal sinus.
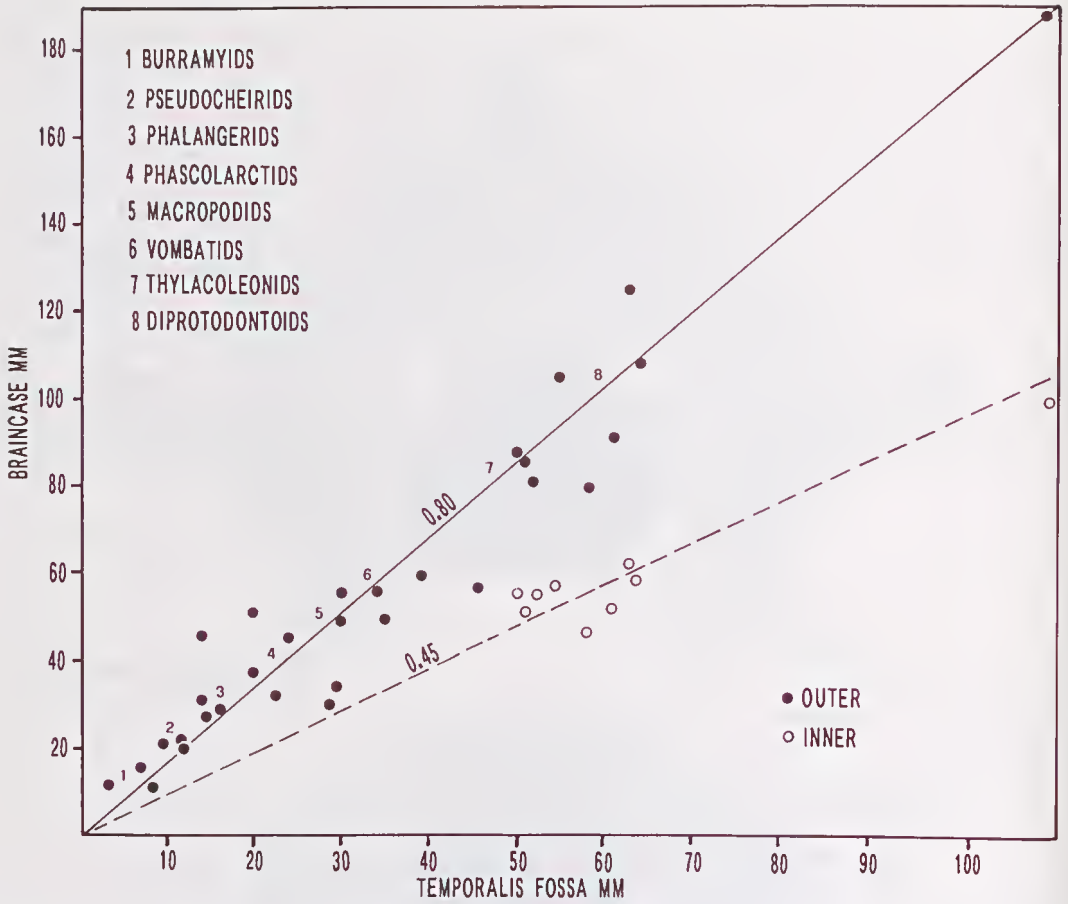
Fig. 6. Scatter diagram depicting differential growth between the outer braincase and neural capsule in a representative series of diprotodontian marsupial genera. The open circles represent the inner braincase width in genera in which there is a significant difference between the inner and outer table diameter. The difference in coefficients between the solid trend line (0.80) and the dashed trend line (0.45) indicate that brain growth is a primary factor in the separation of the inner and outer tables of the brain case.

layer and both surfaces correspond to the contour of the brain. By this encrypted M^4 stage, the brain had reached 4/5 of its maximum volume, establishing the basic extent and form of the inner table of the cranial vault for the remainder of the animal's life. However, the external surface of the cranium of this species will have nearly doubled as the outer table of the neurocranium continues to grow in a linear proportion to the rest of the skull.

The most obvious advantage of the positive allometric growth of the outer table in giant marsupial herbivores is for the support of large adductor muscle masses. An external cranial surface determined by the volume of the relatively small neural capsule in diprotodontids would offer a very reduced surface area for their attachment, which would in any case have re-

quired the development of enormous sagittal and lambdoid crests. The development of a sinus-expanded extracranial surface has the additional advantage of being lighter than solid bony flanges, the air spaces insulate the brain from intramuscular temperature changes (overheating) and could even protect the brain from external trauma.

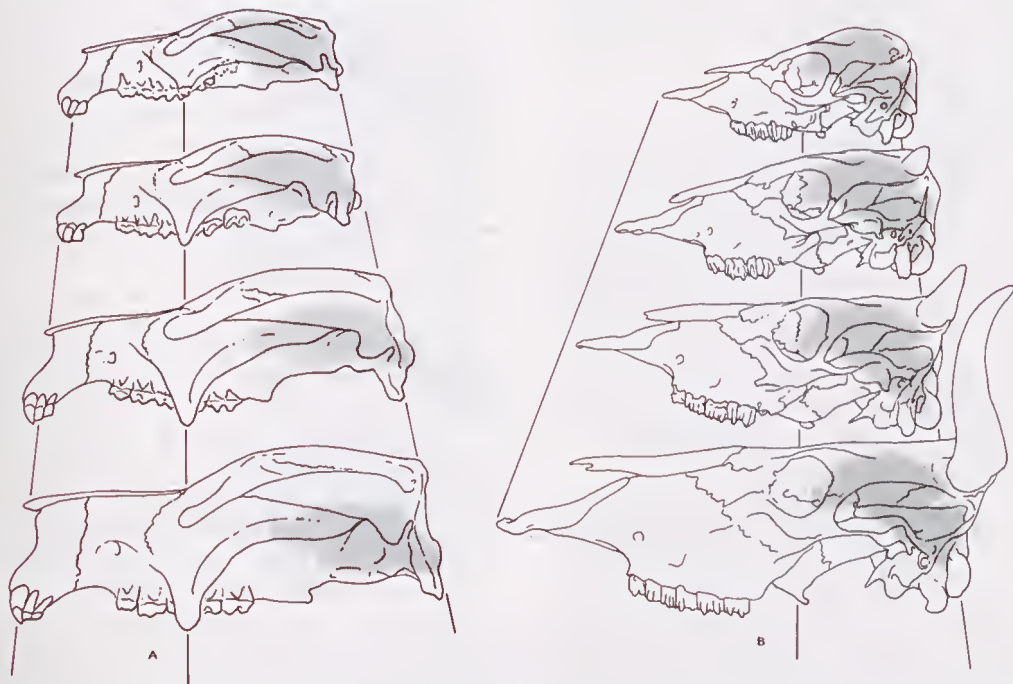## COMPARISON OF MARSUPIAL AND PLACENTAL HERBIVORES

The question remains as to why similar conditions are rare in large placental mammals, many of which show a high degree of proportional sliding between the splanchnocranium and the neurocranium. In the horse and domestic cow for

example, the facial skeleton becomes greatly enlarged in proportion to the neurocranium at maturity, yet there is no apparent equivalent compensatory increase in the surface area for adductor muscle attachment. Factors that seem relevant to this question are: 1) in placentals, the brain volume is generally greater, and the brain continues to expand until later in maturity; 2) the pattern of deciduous tooth replacement is markedly different and the tooth emplacement is relatively farther forward; and 3) the adductor muscle complex emphasizes a contrasting biomechanical pattern.

Brain size and growth. Investigations of marsupial brain size (endocranial volumes or mass) indicate that the diprotodontians (phalangeridans and vombatiformes) have attained brain sizes equivalent to the lower category of middle-ranked placentals (Moeller 1973, Jerison 1973) which consists primarily of large rodents (*Hystrix* Linnaeus, *Castor* Linnaeus, *Marmota* Blumenbach) in Moeller's (1973) sample. The brain mass to body mass ratios in the larger marsupial species are therefore not especially low. However, direct comparison among

very large marsupial and placental species shows the endocranial volume of the marsupial *Zygomaturus trilobus* Mcleay to be approximately 400ml for an estimated body weight of 600kg, whereas the volume of the brain of a 763kg rhinoceros is 655ml (Crile and Quiring 1940). Thus while the differences are probably not great, absolute brain mass may account for some of the tendency for sinus formation in the cranium of large marsupial herbivores.

The factor of continued brain growth during later stages of maturation is difficult to compare because the growth stages of *Kolopsis torus* are not actually known and therefore cannot be directly compared with that of a cow. The endocrania of the cow and horse continue to show a small amount of expansion until they attain full size. Measurements of *Kolopsis* indicate that the endocranium ceases to expand by the time it reaches approximately half its mature cranial dimensions. It is possible, therefore, that the growth of the endocranium in placentals is able to maintain closer proportional growth to the splanchnocranium than its marsupial equivalents.

Fig. 7. Comparison of diprotodontid marsupial and placental herbivore cranial proportions during growth; **A**, a "growth series" of Miocene diprotodontid marsupial *Kolopsis torus* specimens from an encrypted M^1 stage to maturity; **B**, a growth series of the domestic cow, *Bos taurus*. Drawn to approximately equivalent cranial lengths for comparison, cow is actually about 25% larger than *Kolopsis*. Stipple represents the approximate size and shape of the neural capsule; lines compare extent of differential growth. The marsupial outer table growth shows a positive allometry over the splanchnocranium in contrast to the cow in which the splanchnocranium eventually dominates the neurocranium.

Tooth replacement. A primary difference in the development of the splanchnocranium relative to the neurocranium in marsupial and placental herbivores appears to be related to changes in the tooth row. In diprotodontid marsupials the length of the cheek tooth row is practically constant from the "active joey" stage to maturity. In the approximately equivalent postnatal to mature stages of the cow, the cheek tooth row, and consequently the entire facial component of the cranium, changes markedly in relation to the neurocranium. These modifications occur chiefly in relation to the cheek tooth replacement system in placentals, which by contrast to the marsupials is much more complex. Consequently the marsupial splanchnocranium undergoes relatively little proportional change in relation to either its cheek tooth row or its neurocranial component.

Adductor muscle complex. The form of the adductor muscle complex is the most important factor in the differences between large marsupial herbivore and large placental herbivore cranial form. Diprotodontid, palorchestid and even the large carnivorous thylacoleonid *Thylacoleo carnifex* Owen differ substantially from their placental ecomorphic counterparts in retaining a relatively unspecialized adductor complex, classified by Turnbull (1970) as belonging to the Generalized Group.

Turnbull's classification pertains to the extent to which the temporalis, masseter and pterygoideus muscles contribute to jaw closure. In diprotodontids, palorchestids and thylacoleonids the temporalis fossa and surface attachment areas are very large, accounting for 50% or more of the total adductor mass. Felids, the placental equivalents to thylacoleonid marsupials, have Specialized Group I ("carnivore-shear") muscle complexes, and ungulates, the placental equivalents to the diprotodontids, have Specialized Group II ("ungulate-grinding" or "mill" type complexes (Fig. 8).

In the Specialized Group I complex, the temporalis muscle group is decidedly dominant. The muscle complex is characteristic of carnivores with shearing carnassial sets. In Specialized Group II species, the masseter is by far the dominant adductor accompanied by a relatively large pterygoideus contribution. The muscle mass classification of Turnbull (1970) is clearly paralleled by the schematization of jaw mechanics presented by Smith and Savage (1959).

Applied to the forms belonging to Turnbull's specialized groups, the Smith and Savage model closely corresponds. When applied to differentiating the shearing-toothed carnivore *Thylacoleo* from the mill type herbivorous jaws of diprotodontids, the Smith and Savage model produces an ambiguous resolution due to the retention of a generalized adductor muscle complex in the two functional extremes found in the Diprotodontia (Wells *et al.* 1982).

It therefore follows that if the Generalized Group musculature is retained in diprotodontian marsupials, the underlying bony architecture must also be retained, despite the potentially constraining effect of a relatively small internal capsule of the braincase. A relatively small braincase does not constitute a limitation in the Specialized Group II placentals in which the role of the temporalis muscle is significantly reduced.

MACROPODID "EXCEPTIONS"

Large, living macropodid species have nearly the same brain mass to body mass proportions as the vombatids. Moreover, there were some very large extinct macropodids of the genera *Sthenurus* Owen and *Procoptodon* Owen that attained body masses at least two or three times as great as those of the largest living *Macropus* species. If the allometric principle for outer table expansion applies to the Vombatidae, Diprotodontidae and Thylacoleonidae, should it not apply equally to the large macropodids? Obviously it does not, as none of the macropodids, even *Procoptodon goliah* (Owen), the largest species known, had developed large intracranial sinuses surrounding the internal brain capsule.

Measurement of the proportional areas of jaw musculature attachment in large macropodid crania reveals the apparent reason for the lack of conformity in *Macropus*. The temporalis fossa is unusually small and the surface for attachment of the temporalis is reduced compared to diprotodontids (Fig. 8F). Conversely, the m. masseter is large in relation to the m. temporalis and as might be anticipated, the proportions of the jaws conform to the Smith and Savage model of placental herbivore jaw mechanics.

Macropus, Sthenurus and *Procoptodon* are practically unique among marsupials in having a jaw adductor complex corresponding to Turnbull's Specialized group II (Turnbull 1970). Consequently, the absence of an expanded outer table of the neurocranium of large macropodids is anticipated and as such, provides additional evidence in support of the explanation of sinus development in vombatomorphs.

DISCUSSION

Current understanding of these growth and proportional phenomena docs not indicate whether the development of the Speeialized Group II jaw muscle complex represents an evolutionary alternative to positive allometry of the neurocranium in association with increased body size, or invariably, a naturally-selected functional refinement from a gcncralizcd pattern involving a reorganization of the muscle complexes in relation to trophic specializations. Turnbull (1970) eoncludes that mammals, in their course of evolution, tended to utilize the Gencralized Group proportions long after other speeializations had become established (i.e. spc-cialized dentitions) until that configuration no longer sufficed, at whieh point there was a shift over to the approriate Specialized Group pattern.

Among the giant Australian marsupials, selcction for development of compcnsatory sealing adjustments in the neurocranium, in ordcr to rctain a Generalized museular plan has been favoured over a rcorganization of the adductor muscle complex, irrespectivc of the considerable dental specializations found in vombatids, thylacoleonids and diprotodontids. This observation seems to beg the question as to thc dcgree of trophic spccialization neccssary to induce selective pressures that would result in a Speeialized muscular configuration. The rctcntion of a Generalized adductor complex in the majority of marsupials may be related to less stringent competition among browsers and carnivores than
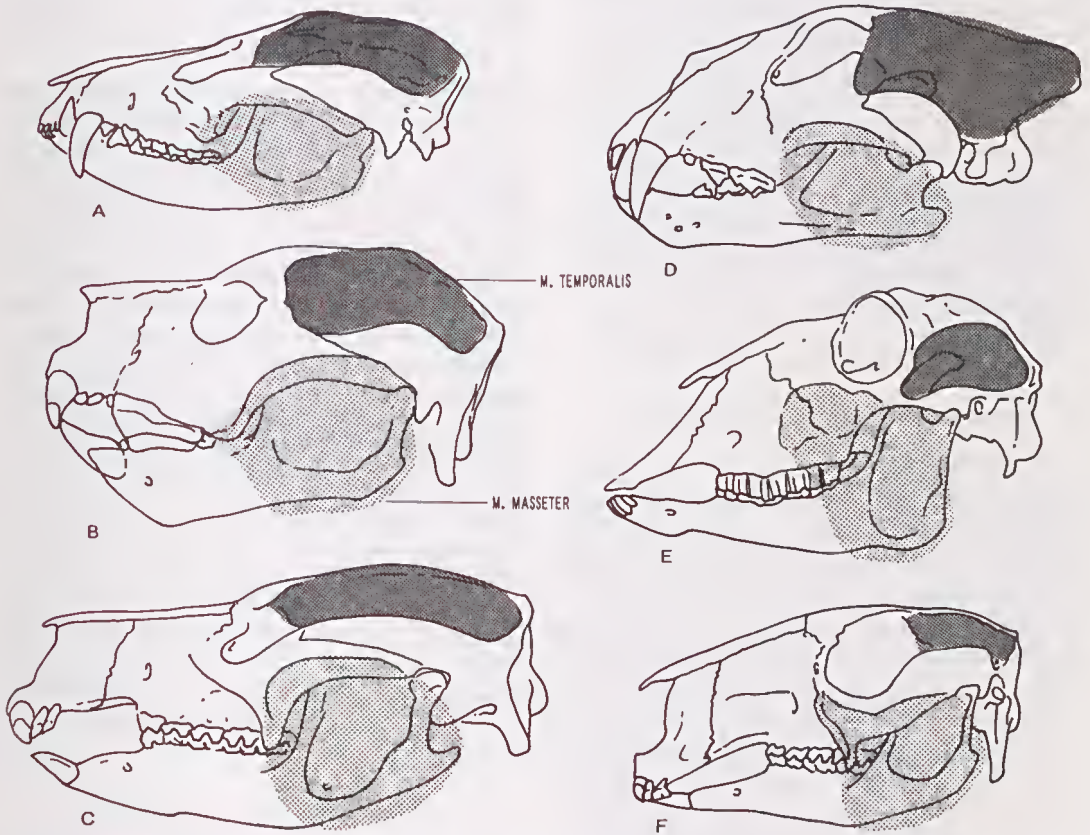

Fig. 8. Drawings of the lateral aspect of marsupial and plaeental skulls eomparing the relative sizes of jaw adductor museles in each species; the dark stipple represents the m. temporalis; the light stipple represents the m. masseter; A, living Virginia opossum *Didelphis virginianus* Kerr; B, Pleistoeene marsupial lion *Thylacoleo carnifex*; C, miocene diprotodontid *Neohelos tirarensis* Stirton; D, living placental lion *Panthera leo* Linnaeus; E, living sheep *Ovis aires* Linnaeus (after Turnbull 1970); F, living red kangaroo (Macropodidae) *Macropus rufus* Desmarest. The large m. temporalis and almost equally large m. masseter contributions in A-C plaees these forms in Turnbull's (1970) Generalized Group; D, the lion, a plaeental carnivore, is an example of the Specialized Group I musele complex in which the m. temporalis is elearly dominant over the m. masseter; E, *Ovis* the placental herbivore, is an example of the Specialized Group II musele complex in whieh the m. masseter is dominant; F, the red kangaroo is decidedly a Speeialized Group II marsupial. The small temporalis musele in Speeialized Group II herbivores does not require expansion of the neurocranial surfaee for its attaehment.

among their placental counterparts, or it may reflect other conditions or restraints of which I am not aware.

The principal modifications of the specialized group adductor musculature pertain to changes in the cross-sectional areas of the muscle masses relative to their points of attachment. In the Generalized Groups, the muscular complexes are predominately broad, oval sections, whereas in the specialized group II muscle complexes, the musculature assumes a more rounded cross-sectional area. However, these gross observations do not provide an adequate explanation of the complexity of the functional modifications involved (Gans and Vree 1987, Gans 1988).

That the Specialized Group II muscle complex has evolved in macropodids but not in diprotodontids, palorchestids or thylacoleonids raises a potentially interesting line of investigation that may be ultimately related to dental evolution in these forms. More detailed studies of some of the parallels between macropodids and Group II placental herbivores may provide new insights into the functional evolution of jaw adductor complexes. Sanson (1989) points out, for example, that the grazing macropodines require very precise occlusion, a feature that might underly the development of specialized adductor systems in all mammals with similar requirements.

SUMMARY AND CONCLUSIONS

Large extinct marsupials of the families Diprotodontidae, Palorchestidae and Thylacoleonidae have highly pneumaticized braincases. The internal capsule of the braincase in these forms is suspended within the outer table by thin septa that correspond to the original parietosquamosal and parietal to parietal contacts. A phylogenetic trend towards this condition is seen in the living wombats in which the cranial vault is greatly thickened, but retains the intervening diploe. It is suggested that vombatids are sufficiently large to reflect a positive allometric relationship of the outer table of the neurocranium to the inner table surrounding the neural cavity. However, large kangaroos, which have about the same brain mass to body mass proportion as vombatids, do not develop a thickend cranial vault.

Previous studies (Gregory 1903, Moss and Young 1960) have demonstrated that the inner and outer tables of the braincase develop independently of one another in accordance with the demands of their associated soft tissue relations. The inner table responds to brain growth and the outer table responds to the supportive requirements of the jaw musculature.

Because the large diprotodontians express an allometry of inner table surface area relative to body size increase, due to brain growth proportional to the cube of its linear dimensions, the neural capsule itself offers inadequate surface area for the attachment of the large jaw adductor musculature, especially the temporalis. The outer table of the braincase responds to the surface area requirements of the temporalis muscle by growing outwards, proportional to the square of its linear dimensions, independantly of the inner table. This process of separation of the inner and outer tables of the neurocranium results in the creation of large air spaces or sinuses between the two laminations of bone.

A similar degree of sinus formation is rare in equivalent- sized placental mammals. The placental herbivores also show a marked difference in the proportioning of their jaw muscle complex, in which the temporalis muscle is greatly reduced, thus eliminating the requirement of a large surface for its attachment. Diprotodontids, palorchestids and thylacoleonids however, retain a generalized or primitive adductor muscle complex in which the temporalis remains as large, or larger than, the masseter, thus necessitating a correspondingly large surface for its attachment.

The large kangaroos represent an exception to the diprotodontian allometric principle. They are unique among diprotodontian marsupials in having developed a specialized jaw adductor complex very similar to that of placental herbivores in which the masseter muscle is dominant to the m. temporalis. The absence of cranial thickening or intracranial sinuses in kangaroos is therefore consistent with the present model.

ACKNOWLEDGEMENTS

REFERENCES

Aplin, K. 1987. Basicranial anatomy of the early Miocene diprotodontian *Wynyardia bassiana* (Marsupialia, Wynyardiidae) and its implications for wynyardiid classification and evolution. In: Archer, M. (cd.) *Possums and opossums: studies in evolution.* Pp. 369-391. Surrey Beatty & Sons and the Royal Zoological Society of New South Wales: Sydney.

Aplin, K. and Archer, M. 1987. Recent advances in marsupial systematics with a new syncretic classification. In: Archer, M. (cd.) *Possums and opossums: studies in evolution.* pp xv-lxxii. Surrey Beatty & Sons and the Royal Zoological Society of New South Wales: Sydney.

Crile, G. and Quiring, D. 1940. A record of the body weight and certain organ and gland weights of 3690 animals. *Ohio Journal of Science* **XL**(5): 219-259.

Gans, C. 1988. Muscle insertions do not incur mechanical advantage. *Acta Zoologica Cracoviensia* **31**(25):615-624.

Gans, C. and de Vree, F. 1987. Functional bases of fibre length and angulation in muscle. *Journal of Morphology* **192**:63-85.

Gregory, W.K. 1903. Adaptive significance of the shortening of the elephant's skull. *Bulletin of the American Museum of Natural History* **387**.

Gregory, W.K. 1974. *Evolution Emerging, Vol II.* Arno Press: New York, New York.

Jerison, H. 1973. *Evolution of the brain and intelligence.* Academic Press: New York.

Klaauw, C.J. van der, 1931. The auditory bulla in some fossil mammals. *Bulletin of the American Museum of Natural History* **LXII**:1-341.

Klaauw, C.J. van der, 1946. Cerebral skull and facial skull. *Archives Neerlandaises de Zoologie* **7**:16-37.

Klaauw, C.J. van der, 1948-52. Size and position of functional components of the skull. *Archives Neerlandaises de Zoologie* **9**:1-559.

Moeller, H. 1973. Zur Evolutionshohe des Marsupialiagehirns. *Zoologische Jahrbücher (Anatomie) Bd.* **91**:434-448.

Moss, M. and Young, R. 1960. A functional approach to craniology. *American Journal of Physical Anthropology* **23**:261-276.

Osborne, H. 1942. Proboscidea: A monograph of discovery, evolution, migration and extinction of mastodonts and elephants of the world, Vol II. *American Museum Natural History Monograph.*

Owen, R. 1877. *On the fossil mammals of Australia, with a notice of the extinct marsupials of England, Vol. II.* J. Erxleben: London.

Ride, W.D. 1964. A review of Australian fossil marsupials. *Journal and Proceedings of the Royal Society of Western Australia* **47**: 97-131.

Sanson, G. 1989. Morphological adaptations of teeth to diets and feeding in the Macropodoidca. In: Grigg, G., Jarman, P. and Hume, I. (eds) *Kangaroos, wallabies and rat kangaroos.* Pp 151-168. Surrey Beatty & Sons: Sydney.

Smith, J.M. and Savage, R.J. 1959. The mechanics of mammalian jaws. *School Science Reviews* **40**:289-301.

Turnbull, W.D. 1970. Mammalian masticatory apparatus. *Fieldiana: Geology* **18**(2):149-356.

Wells, R., Horton D. and Rogers, P. 1982. *Thylacoleo carnifex* Owen (Thylacoleonidae): marsupial carnivore? In: M. Archer (ed.) *Carnivorous marsupials*, (Vol. 2). Pp. 573-586. Royal Zoological Society of New South Wales: Sydney.